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Atmospheric CO_2 Uptake by *Pinus densiflora* and *Quercus mongolica*

Hyun-Kil Jo and Tae-Won Ahn*

Landscape Architecture Program, College of Forest Science, Kangwon National Univ., Chuncheon 200-701, Korea
**Dept. of Landscape Architecture, Graduate School, Kangwon National University, Chuncheon 200-701, Korea*

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Plants sequester atmospheric CO_2, a major agent of climate change, during the growing periods and mitigate its rising accumulation in the atmosphere. *Pinus densiflora* and *Quercus mongolica* are the native tree species dominant in the temperate forests of Korea. This study quantified the annual CO_2 uptake by the two species at forest sites in Chuncheon in the middle of the country. The quantification was based on seasonal measurements of CO_2 exchange rates under natural conditions by an infrared gas analyzer over the growing season (1999). The monthly CO_2 uptake per unit leaf area ranged from 1.6-6.7 $mg/dm^2/h$ for *P. densiflora* and from 3.7-8.9 $mg/dm^2/h$ for *Q. mongolica*, with a maximum in mid-summer. An equation for each species was generated to estimate easily the annual CO_2 uptake by total leaf area per tree, which subtracted the CO_2 release (i.e. respiration) by leaves and woody organs from the gross CO_2 uptake (diurnal uptake and release by leaves). Annual CO_2 release by leaves and woody organs accounted for 58-73% of the gross CO_2 uptake across tree specimens. Annual CO_2 uptake per tree increased with increasing dbh (stem diameter at breast height) for the study diameter range, and was greater for *Q. mongolica* than for *P. densiflora* in the same dbh sizes. This was mainly associated with a greater total leaf area in the former. For example, the annual CO_2 uptake by one tree with dbh of 25 cm was 35.6 kg/yr for *P. densiflora* and 47.9 kg/yr for *Q. mongolica*. The results from this study can be applied to evaluate an atmospheric CO_2 reduction of woody plants by forest type and age class.

Key words: Climate change, CO_2 budget, Dominant species, Leaf area, Equation, Korea

1. Introduction

Carbon dioxide is a major greenhouse gas causing climate change[1,2] which is one of the most serious environmental concerns of the world. The atmospheric CO_2 concentration is currently increasing by about 0.4% per year[1,3]. This increase is primarily due to fossil fuel combustion and deforestation. Trees sequester atmospheric CO_2 through photosynthesis during the growing periods, and thus mitigate its rising accumulation in the atmosphere.

Annual CO_2 uptake by trees can be estimated by an examination of the annual biomass increment from harvesting or stem coring and its conversion to CO_2 fixation[4,5]. There are limitations in this method found in obtaining an efficient sample size where tree cutting is limited and in exploring changes of seasonal CO_2 uptake. Another way to overcome the limitations is by direct measurements of the annual CO_2 exchange of trees using an infrared gas analyzer. However, many previous studies for the direct CO_2 measurement were conducted under controlled environments over a short term[6,7]. Little information has been collected on CO_2 exchange of adult trees under natural conditions over growing seasons. Contrary to crops, the size and logevity of trees make it very difficult to measure CO_2 exchange accurately at the canopy level over a long term.

Pinus densiflora Sieb. et Zucc. and *Quercus mongolica* Fisch., which are evergreen and

Corresponding Author : Hyun-Kil Jo, Landscape Architecture Program, College of Forest Science, Kangwon National Univ., Chuncheon 200-701, Korea
Phone : +82-33-250-8345
E-mail : jhk@kangwon.ac.kr

deciduous, respectively, are the native tree species dominant in temperate forests of Korea[8,9]. Deforestation will return CO_2 fixed by forests to the atmosphere. Information on annual CO_2 uptake by these species is essential to evaluate their environmental importance in atmospheric CO_2 reduction and to control a significant loss of stored CO_2 from forest damage. The purpose of this study was to quantify annual CO_2 uptake by *P. densiflora* and *Q. mongolica*, based on measurements of CO_2 exchange rates by an infrared gas analyzer.

2. Methods

2.1. Measurement of CO_2 exchange rate and environmental parameter

Six normally growing specimens of *P. densiflora* and *Q. mongolica* (3 specimens of each species) were selected at forest sites of Chuncheon in the middle of Korea (latitude: 37° 52', longitude: 127° 45'), based on differences in slope direction and incoming radiation. The tree specimens were not located very far from each other to save time and labor for the periodical moving of measurements. Monthly CO_2 exchange rates of leaves of the two species were measured under natural conditions over the growing season(1999) using a portable infrared gas analyzer (LI-COR LI-6400, Nebraska). Carbon dioxide uptake was measured with 20 replicates every 1.5-hour interval from 8:00 to 17:00 in the middle part of each month, while CO_2 release (i.e. respiration) was done every 3-hour interval from 8:00 to 23:00. Representative leaf specimens, as placed around the middle of tree crowns, were randomly chosen for the measurements so that leaf age and light intensity could be matched at each measuring time.

Photon flux density (PFD), air temperature, and relative humidity affecting CO_2 exchange rates of the 6 specimens were measured at 3-hour intervals for 24 hours from 8:00 (only during daytime for PFD) in the early, middle, and late part of each month over the growing season. PFD at the middle of both the outer and inner tree crowns was measured with a quantum sensor (LI-COR LI-190SA, Nebraska) in their 8 directions (north, northeast, east, southeast, south, southwest, west, and northwest) to reflect changes in incoming radiation. Temperature and humidity around the tree crowns were measured using an automatic measuring instrument (HOBO H08-032-02, Massachusetts).

2.2. Measurement of leaf area

To produce a CO_2 exchange rate per tree from the rate measured on an unit leaf-area basis, a monthly leaf area of the 6 specimens was obtained by measuring the leaf area index (LAI) with a plant canopy analyzer (LI-COR LAI-2000, Nebraska) in the middle part of each month. The measurements of LAI were taken from 4 directions of the tree crowns, with 8 repetitions for each direction, around sunset or sunrise, to preclude any underestimation of LAI associated with direct sunlight. In addition, LAI of about 30 trees for each species which were randomly sampled around the study sites to represent the range of stem diameters, were measured in September to obtain regression equations for calculating the total leaf area per tree in the late growing season. An iterative linear and nonlinear approach was applied to determine the most appropriate parameters (e.g. stem diameter, crown volume) and equation for leaf area estimation.

2.3. Measurement of branch respiration

A Seasonal branch respiration of the study species was measured in May, July, and October with a portable infrared gas analyzer (LI-COR LI-6400, Nebraska). For each species and each month, 11 to 17 branch specimens which represented diverse diameter sizes, were cut to an adequate size in order to be put into the chamber (LI-COR LI-6400-09) of the infrared gas analyzer. Right after cutting, cut parts of the branch specimens were attached with an airproof tape and their respiration per unit hour was measured in the field. The branch specimens were bagged, transported to the laboratory, and oven-dried at 65°C to constant weight to obtain respiration rates per unit dry weight.

2.4. Estimation of annual CO_2 uptake

Regression equations to estimate seasonal CO_2 exchange rates per unit of hour and leaf area were generated using as independent variables PFD, temperature, and humidity which were recorded simultaneously with each measurement of CO_2 exchange rates by the infrared gas analyzer. A repetitive linear and nonlinear approach was used to determine the most appropriate parameters and equation for each species. The environmental parameters including the PFD at 16 spots of tree crowns which were measured hourly in the early, middle, and late part of each month, were applied to the equations derived to compute the mean monthly CO_2 exchange rates per unit of hour and leaf area. These monthly rates were multiplied by monthly daytime or night time length, except rainy days, and then by monthly leaf area, in order to obtain the total monthly CO_2 uptake or release by leaves.

Regression equations to estimate the total branch weight of each species were derived from the existing literature[4]. Branch respiration measured per unit of hour and dry weight was multiplyed by estimates of the total branch weight from the equations and by the time length of each growing season to generate the total seasonal branch respiration. Based on the average respiration ratios of branches and other non-photosynthetic organs[10,11], the respiration of stems and roots was calculated by multiplying the branch respiration by 0.7 and 0.3, respectively.

Monthly CO_2 exchange was integrated over the entire growing season to obtain an annual CO_2 exchange, and the annual CO_2 release by leaves and woody parts were subtracted from the annual CO_2 exchange to generate an annual CO_2 uptake of the 6 tree specimens. An equation to estimate easily the annual CO_2 uptake per tree of each species was derived from the establishment of the following conceptual formula:

$$\text{Annual } CO_2 \text{ uptake} = (TLA \times ACU \times CF) - (TBW \times AR)$$

where: TLA=equation for total leaf area of late growing season, ACU=annual CO_2 uptake per unit leaf area, CF=correction factor reflecting monthly changes of total leaf area, TBW= equation for total branch weight, and AR= annual respiration of woody organs per unit branch weight).

In the formula, estimating the total leaf area during the late growing season was considered to preclude a heavy amount of work to measure the monthly changes of the total leaf area for general use of the CO_2 uptake equation. ACU and CF were calculated by averaging values from the 3 tree specimens of each species. It was assumed that there was little CO_2 exchange during winter, freeze-up.

3. Results and Discussion

3.1. Growing conditions of tree specimens

Stem diameter at a breast height (dbh) of 1.2 m of the 6 tree specimens ranged from 15 to 28 cm. The crown volume was between 20 to 24 m^3 for *P. densiflora* and 52 to 140 m^3 for *Q. mongolica* (Table 1). Average monthly maximum PFD irradiated at outer tree crowns was highest in July, with values of 1,420-1,780 umol/m^2/s across the species and growing places (Fig. 1). Average seasonal maximum PFD was lowest in fall, with a value of about a half of that in summer. Minimum PFD at inner tree crowns, which reflects canopy density, was 3-7% of the maximum PFD over the growing seasons for *P. densiflora* and 2-4% for *Q. mongolica*. The minimum PFD was slightly higher for the former than for the latter, due to the clustering effect of needles allowing for a deeper penetration of light into the canopy.

Temperature and humidity around the tree crowns during the 6 months from May-October averaged about 20.4°C and 73%, respectively, for all tree specimens. Monthly temperature and humidity were at a maximum in August with an average of 25.1°C and 80%. The concen-

Table 1. Dimensions and growing places of tree specimens for each species selected to measure CO_2 exchange rates and environmental parameters

Species	Place*	Dbh** (cm)	Tree height (m)	Crown Width (m)	Crown Volume (m³)
Pinus densiflora	S	14.5	7.5	5.2	23.3
	W	15.1	9.2	4.7	24.3
	N	18.2	8.3	4.8	19.9
Quercus mongolica	S	16.5	9.9	5.5	51.9
	Top	21.1	10.4	7.2	108.4
	E	27.7	11.6	7.4	140.0

* Expressed as slope directions (the same with Fig. 1)
** Stem diameter at breast height of 1.2m (the same with Fig. 2 and subsequent tables)

tration of atmospheric CO_2 averaged about 380 ppm at their growing places over the growing season. Its concentration was lower in summer than in spring or fall, probably due to a greater photosynthetic CO_2 uptake in summer. Forest soils in Chuncheon including study sites were gravelly loams or sandy loams[12]. Organic matter and moisture in these soils averaged 1.0% and 8.3%, respectively.

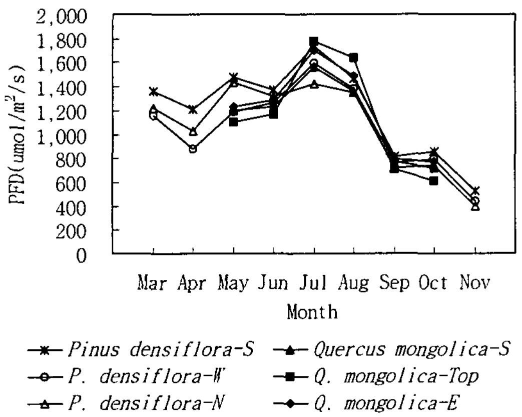

Fig. 1. Monthly changes of maximum photon flux density (PFD) at crowns of tree specimens in different settings.

3.2. Seasonal CO_2 exchange rate at the crown level

Carbon dioxide exchange rates of a crown are the integration of photosynthetic CO_2 uptake and respiratory CO_2 release by all leaves that compose the crown. They are influenced not merely by photosynthetic capacity and total area of leaves, but also by environmental factors such as irradiation, temperature, and humidity. Table 2 lists regression equations for each species to estimate seasonal CO_2 exchange rates per unit of hour and leaf area applying environmental parameters. All the equations had r^2 values greater than 0.74 (a maximum of 0.94), and were statistically significant (P<0.05) as indicated by the F test. Monthly CO_2 exchange

Table 2. Regression equations for each species generated to estimate seasonal CO_2 exchange rates by leaves (μmol/m²/s)

Species	Season	Equation*	r^2	P	n
Pinus	Spring	$\ln Y_1=-6.3605+0.5271\ \ln X+0.3734\ \ln Y+0.9428\ \ln Z$	0.74	<0.001	19
densiflora	(3-5)	$Y_2=-0.4700+0.0165\ X-8.07E-6\ X^2$	0.83	<0.001	25
		$\ln Y_3=-4.3058+1.6119\ \ln Y-0.2556\ \ln Z$	0.83	<0.001	11
	Summer	$\ln Y_1=-2.4460+0.4956\ \ln X-1.2931\ \ln Y+1.3008\ \ln Z$	0.81	<0.001	19
	(6-8)	$Y_2=-0.6122+0.0112\ X-4.02E-6\ X^2$	0.78	<0.001	25
		$\ln Y_3=-10.9275+2.7270\ \ln Y+0.4718\ \ln Z$	0.86	<0.001	12
	Autumn	$\ln Y_1=-4.8060+0.6682\ \ln X+0.0674\ \ln Y+0.5584\ \ln Z$	0.94	<0.001	19
	(9-11)	$Y_2=-0.3462+0.0187\ X-7.92E-6\ X^2$	0.76	<0.001	26
		$\ln Y_3=-4.5684+0.6729\ \ln Y+0.6250\ \ln Z$	0.85	<0.001	11
Quercus	Spring	$\ln Y_1=-12.5817+0.6899\ \ln X+0.5956\ \ln Y+2.0435\ \ln Z$	0.83	<0.001	14
mongolica	(5-6)	$Y_2=-1.1444+0.0225\ X-1.10E-5\ X^2$	0.77	<0.001	17
		$\ln Y_3=-2.4894+0.9832\ \ln Y-0.0834\ \ln Z$	0.79	0.004	8
	Summer	$\ln Y_1=-8.8050+0.9380\ \ln X-0.1311\ \ln Y+1.2582\ \ln Z$	0.86	<0.001	14
	(7-8)	$Y_2=-0.7344+0.0176\ X-5.99E-6\ X^2$	0.91	<0.001	17
		$\ln Y_3=-9.3713+2.8199\ \ln Y+0.1098\ \ln Z$	0.74	0.033	7
	Autumn	$\ln Y_1=-2.1937+0.6775\ \ln X-0.3082\ \ln Y+0.0965\ \ln Z$	0.92	<0.001	13
	(9-10)	$Y_2=-0.5724+0.0165\ X-7.70E-6\ X^2$	0.82	<0.001	17
		$\ln Y_3=-7.0962+2.6994\ \ln Y-0.3637\ \ln Z$	0.90	0.003	8

* Y_1: Uptake, Y_2: Uptake and nocturnal release, Y_3: Diurnal release,
X : PFD (μmol/m²/s), Y : Temperature (℃), Z : Humidity (%)

rates at the crown level were computed using the equations, as shown in Table 3 (average values from the 3 specimens for each species). The monthly CO_2 uptake is an estimate averaged from the two equations of Y_1 and Y_2 in Table 2.

Photosynthetic CO_2 uptake at the crown level of the two species tended to be higher in middle summer, and lower in early spring and late fall when temperatures were lower. *Q. mongolica* showed a higher CO_2 uptake from June to August than did *P. densiflora* ($P<0.01$). Ceulemans and Saugier[7] also showed that the photosynthetic capacity of most conifers was lower than that of deciduous broad-leaved trees, which was found under optimal light and temperature conditions. There was no significant difference ($P>0.05$) between the two species in the CO_2 uptake over the entire growing season, due to relatively lower photosynthetic capacity in the early and late growing season of *Q. mongolica*. Diurnal or nocturnal CO_2 release by leaves of both species was not greater than 2.5 mg/dm^2/h for each month, although it showed some seasonal variation. In comparison, seasonal CO_2 uptakes and releases by *Ginkgo biloba* Linné, one of the popular landscape tree species in the cities of Korea, were reported to be a

Table 3. Monthly CO_2 exchange rates at the crown level for each species (mg/dm²/h)

Species	Month	Uptake	Release	
			Diurnal	Nocturnal
Pinus	Mar	1.59	0.16	0.72
densiflora	Apr	5.24	0.70	0.72
	May	5.62	1.18	0.72
	Jun	6.30	1.32	1.12
	Jul	6.74	1.70	1.12
	Aug	5.72	1.81	1.12
	Sep	5.11	2.03	0.72
	Oct	5.06	1.20	0.72
	Nov	2.75	0.75	0.72
Quercus	May	4.21	1.83	1.70
mongolica	Jun	8.01	2.19	1.70
	Jul	8.88	2.31	1.22
	Aug	7.42	2.47	1.22
	Sep	3.89	1.48	0.94
	Oct	3.66	0.41	0.94

maximum of about 12 mg/dm^2/h and 2 mg/dm^2/h during summer, respectively[13]. Maximum seasonal CO_2 uptake by *Q. mongolica* (about 9 mg/dm^2/h) was lower than that of *G. biloba*.

3.3. Total leaf area per tree

Fig. 2 shows regression equations for each species for calculating total leaf area per tree of the late growing season and trends of the total leaf area by dbh growth. The equations had relatively high r^2 values, 0.92 for *P. densiflora* and 0.88 for *Q. mongolica*, and were all statistically significant ($P<0.0001$). The dbh of sample trees ranged from 5 to 29 cm for *P. densiflora* and from 4 to 30 cm for *Q. mongolica*. Although the LAI of both species was similar with a range of 3-4, the total leaf area of *Q. mongolica* was 1.8-2.0 times greater than that of *P. densiflora* for the same dbh sizes. This was due to a greater crown size in *Q. mongolica*, compared to *P. densiflora*.

3.4. Branch respiration

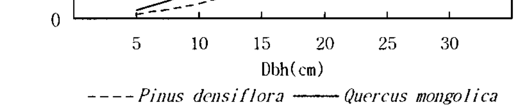

Fig. 2. Trends of total leaf area per tree by dbh growth for each species.

Respiration rates of branches per unit dry weight varied seasonally, with an average of 0.06-0.13 mgCO_2/g/h for *P. densiflora* and 0.08-0.18 mgCO_2/g/h for *Q. mongolica* (Table 4). The seasonal branch respiration of both species was lower ($P<0.05$) in spring and autumn than in summer when temperatures were higher. However, there was no significant difference ($P=0.38$) in the branch respiration of *P. densiflora* between summer and autumn. In spring and summer, *Q. mongolica* showed a

Table 4. Seasonal respiration rates of branches for each species

Season	Species	Diameter range(cm)	Temperature* (℃)	Respiration* ($mgCO_2/g/h$)	n
Spring	*Pinus desiflora*	0.8- 8.5	21.8±0.2	0.062±0.007	13
	Quercus mongolica	1.2- 8.0	22.2±0.2	0.131±0.018	11
Summer	*Pinus desiflora*	1.1- 9.2	32.6±0.2	0.128±0.011	17
	Quercus mongolica	1.8-10.1	33.8±0.2	0.179±0.018	15
Autumn	*Pinus desiflora*	1.2- 9.9	18.7±0.1	0.124±0.008	16
	Quercus mongolica	1.0- 9.8	17.2±0.2	0.078±0.007	16

* Mean±standard error

higher branch respiration than did *P. densiflora* ($P<0.05$), but *vice versa* in autumn ($P<0.01$). This result implies that the branch tissues of the evergreen *P. densiflora* could be physiologically active even in the late growing season of deciduous tree species. Han *et al.*[14] found that the branch respiration rates of 6 to 10-year old *P. densiflora* saplings averaged about 0.08 $mgCO_2/g/h$ at a controlled temperature of 18°C. The average branch respiration of both spring and autumn from this study for the same species (0.09 $mgCO_2/g/h$) was similar to that of Han's study.

Regression equations for each species for estimating the total dry weight of branches per tree[4] are presented in Table 5. The equations had r^2 values of 0.98-0.99, which indicate strong relationships between the branch weight and the independent variable of dbh. The dbh range of sample trees, from which the equations were derived, was 6-43 cm across the two species. Total branch weight per tree of *Q. mongolica* was about 2 times greater than that of *P. densiflora* for the same dbh sizes. Differences in the branch weight between the two species tended to increase with dbh growth.

Table 5. Regression equations for each species generated to calculate total dry weight of branches per tree (kg)[4]

Species	Dbh range (cm)	Equation	r^2
Pinus densiflora	6.4-42.9	lnY=-4.2318+2.4175 lndbh	0.99
Quercus mongolica	6.0-42.0	lnY=-3.5054+2.4017 lndbh	0.98

3.5. Annual CO_2 uptake per tree

The annual exchange and net uptake of CO_2 per tree for the study specimens are summarized in Table 6. Annual CO_2 uptake per tree, which subtracted CO_2 release by leaves and woody parts from the gross CO_2 uptake (diurnal uptake and release by leaves), ranged from 14.7-21.5 kg/yr for the specimens of *P. densiflora* and from 20.9-81.9 kg/yr for those of *Q. mongolica*, varying with dbh sizes. Diurnal and nocturnal CO_2 release by leaves accounted for 31-38% of gross CO_2 uptake across the specimens, and total CO_2 release by woody parts as well as leaves occupied 58-73% of gross CO_2 uptake.

Table 7 lists equations for each species generated to calculate annual CO_2 uptake per tree. Explaining the equation for *P. densiflora* as an example, the value of 1.0613 is the annual CO_2 uptake per unit leaf area, and 0.8519 is the correction factor that reflects monthly changes of total leaf area. The coefficient of 0.8519 corrects a CO_2 uptake estimate from the use of total leaf area of the

Table 6. Annual CO_2 budget per tree for study specimens (kg/tree/yr)

Species	Dbh (cm)	Foliage: Gross uptake*	Foliage: Release	Woody release	Net uptake
Pinus densiflora	14.5	35.0	11.2	9.0	14.8
	15.1	36.3	11.7	9.9	14.7
	18.2	52.9	16.5	14.9	21.5
Quercus mongolica	16.5	75.1	28.9	25.3	20.9
	21.1	124.8	44.9	45.7	34.2
	27.7	246.5	76.8	87.9	81.9

* Diurnal uptake and release

Table 7. Equations for each species generated to calculate annual CO_2 uptake per tree(kg)

Species	Equation
Pinus densiflora	$e^{(-1.6799+1.8474\ \ln dbh)} \times 1.0613 \times 0.8519 - e^{(-4.2318+2.4175\ \ln dbh)} \times 0.8299$
Quercus mongolica	$e^{(-1.1713+1.8919\ \ln dbh)} \times 0.8545 \times 0.9974 - e^{(-3.5054+2.4017\ \ln dbh)} \times 1.0044$

late growing season alone. The value of 0.8299 is the annual respiration of woody organs per unit branch weight.

Based on the above-mentioned equations, the annual CO_2 uptake per tree by *P. densiflora* and *Q. mongolica* increased with increaing dbh (Table 8), and it was greater for *Q. mongolica* than for *P. densiflora* for the same dbh sizes (1.5 times greater at a maximum across dbh classes). This difference, however, gradually decreased in dbh range of more than 30 cm, largely due to a higher CO_2 release by woody parts of *Q. mongolica*. Assuming that gasoline consumption of 1 L (liter) emits about 2.2 kg of CO_2[15], annual CO_2 uptake by one tree with a dbh of 25 cm equaled the amount of CO_2 emitted from gasoline use of approximately 16 L for *P. densiflora* and 22 L for *Q. mongolica*. The annual CO_2 uptake at the per tree level from this study can be applied to evaluate, through measurements of dbh and density, an atmospheric CO_2 reduction at the unit area level of woody plants by forest type and age class.

Table 8. Indicator of annual CO_2 uptake at the per tree level by dbh growth for each species (kg/tree/yr)

Species	Dbh (cm)							
	5	10	15	20	25	30	35	40
Pinus densiflora	2.7	8.7	16.7	25.8	35.6	45.4	54.8	63.6
Quercus mongolica	4.1	13.0	24.2	36.2	47.9	58.2	66.2	71.3

4. Conclusions

Carbon dioxide is a major greenhouse gas causing climate change. This study quantified annual CO_2 uptake by *P. densiflora* and *Q. mongolica*, the native tree species dominant in temperate forests of Korea. Estimating their annual uptake was based on seasonal measurements of CO_2 exchange rates under natural conditions by an infrared gas analyzer over the growing season. This study breaks new ground by tackling the difficulty of taking monthly field measurements of CO_2 exchanges for trees and the complexity associated with the quantification of an annual CO_2 uptake.

Monthly CO_2 uptake per unit leaf area ranged from 1.6-6.7 $mg/dm^2/h$ for *P. densiflora* and from 3.7-8.9 $mg/dm^2/h$ for *Q. mongolica*, with a peak in the middle of summer. Annual CO_2 uptake by total leaf area per tree, which subtracted a CO_2 release from the gross uptake, ranged from 14.7- 21.5 kg/yr for *P. densiflora* specimens and from 20.9-81.9 kg/yr for *Q. mongolica* specimens, varying with dbh sizes. Annual CO_2 release by leaves and woody parts accounted for 58-73% of the gross CO_2 uptake across the specimens.

An equation for each species was generated to estimate the annual CO_2 uptake per tree easily, using dbh as an independent variable. The equations can be applied to evaluate an atmospheric CO_2 reduction at the unit area level by forest type and age class. Annual CO_2 uptake by a tree with dbh of 25 cm equaled the amount of CO_2 emitted from gasoline consumption of about 16 L for *P. densiflora* and 22 L for *Q. mongolica*. The results from this study are expected to be useful for estimating environmental values in atmospheric CO_2 reduction of the tree species.

This study put emphasis on quantifying the annual CO_2 uptake at the per tree level, based on monthly measurements of CO_2 exchange at the leaf level. There could be partial limitations of this method in generalizing actual CO_2 exchange at the crown level. Respiration of stems and roots was estimated by applying data from the literature, because taking actual respiration measurements is difficult. Estimates of annual CO_2 uptake from this study need to be tested by devising other valid methods in the future.

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